9 Balanced networks: Noise, synaptic scaling, and linear response

An interesting observation is that the subthreshold neuronal voltage in cortical neurons is very noisy. Naively, one might expect that the subthreshold potential would be noisy if there were relatively few inputs, consistent with the notion of a few strong inputs that one sees in cortical slice experiments. But the other possibility is that the input is so noisy because large excitatory inputs are offset by large inhibitory inputs, so that their mean value just about cancels but the variances, of course, add. The notion of large offsetting currents comes from the intracellular recording experiments in cat V1 from pioneering experiments in the laboratories of Ferster, Fregnac, and Douglas with recent contributions from mouse by Isaacson. In general, excitatory and inhibitory inputs are found to be both large and have the same tuning curves, so that their inputs act to balance each other. The gain from offsetting currents is that a transient increase in excitatory input, as may occur with a large burst of input, will rapidly depolarize the cell. So balanced networks trade noise for speed.

9.1 Variability for a single cell

9.1.1 Weak synaptic inputs

Let’s start with a warm up on scale of noise in the input. First, some definitions. The input to cell \(i\) from cell \(j\) is \(W_{ij}\) with \(j = 1, 2, \ldots, N\), while the output of the neuron is taken as \(V_i\) with \(i = 1, 2, \ldots, N\) where \(V = \frac{1}{2}(S + 1)\) is a Bernoulli variable with \(V = 1\) if the cell spikes and \(V = 0\) if it does not. Let’s say that the probability that a cell is spiking is \(m\), so that \(V = 1\) with probability \(m\) and \(V = 0\) with probability \(1 - m\). The input to the \(i\)-th neuron is:

\[
\mu_i(t) \equiv \frac{1}{N} \sum_{j=1}^{N} W_{ij} V_j(t). \quad (9.1)
\]

The standard thermodynamic scaling, so that total synaptic currents are bounded as the size of the system increases, is that each input has a strength of order 1. For simplicity, let’s take all of the inputs to be equal, so

\[
W_{ij} \to W_o. \quad (9.2)
\]

The \(W_o\) are of order 1 so the inputs are of order 1, with

\[
\mu_i(t) = W_o \frac{1}{N} \sum_{j=1}^{N} V_j(t). \quad (9.3)
\]
where \( m(t) \) is the average across the network, i.e.,

\[
m(t) \equiv \frac{1}{N} \sum_{j=1}^{N} V_j(t) \quad (9.4)
\]

and is of order 1. Clearly, for constant connections, the input to all neurons is equal so the population average is

\[
\mu(t) \equiv \frac{1}{N} \sum_{i=1}^{N} \mu_i(t) = W_o m(t) \quad (9.5)
\]

and the time average is

\[
\langle \mu \rangle \equiv \frac{1}{T} \int_{-T/2}^{T/2} dt \mu_i(t) = W_o m \quad (9.6)
\]

The variance across time is

\[
\sigma_i^2 = \langle (\mu_i(t) - \langle \mu \rangle)^2 \rangle = \left[ \langle \mu_i^2 \rangle - \langle \mu \rangle^2 \right] = \langle \mu_i^2 \rangle - W_o^2 m^2. \quad (9.7)
\]

We evaluate the first term under the assumption that the correlations in the neuronal outputs are zero, i.e.,

\[
\langle \mu_i^2 \rangle = \left\langle \frac{W_o^2}{N^2} \sum_{i=1}^{N} \sum_{j=1}^{N} V_i(t)V_j(t) \right\rangle = \frac{W_o^2}{N^2} \left\langle \frac{1}{N^2} \sum_{i=1}^{N} V_i(t) \right\rangle + \frac{1}{N^2} \sum_{i=1}^{N} \sum_{j \neq i}^{N} V_i(t)V_j(t) = \frac{W_o^2}{N} \langle m(t) \rangle + W_o^2 \left( 1 - \frac{1}{N} \right) \langle m^2(t) \rangle = \frac{W_o^2}{N} (m - m^2) + W_o^2 m^2 \quad (9.8)
\]

and thus

\[
\sigma_i^2 = \frac{W_o^2}{N} m(1 - m). \quad (9.10)
\]

The variance for the population is the same, i.e.,

\[
\sigma^2 = \frac{W_o^2}{N} m(1 - m). \quad (9.11)
\]
We see that for large networks the mean level drives the spiking and the variability goes to zero as $1/N$. As expected for a binomial variable, the variance is also zero when all neurons are active, i.e., $m = 1$, or quiescent, i.e., $m = 0$. Lastly, for a poisson process, $\sigma^2 = \frac{W_o^2}{N}m$ where $m =$ rate $X$ time interval.

9.1.2 Strong synaptic inputs

How can we have a network with high noise? Let’s recall the issue of networks with a small fraction of strong connections. The challenge is to recast the input so that the variance does not diminish to zero as a function of the number of input neurons. This is where the idea of balance comes into play.

1. We need the input to be the sums of two terms, one excitatory and one inhibitory

2. We need the total current from these two term to cancel, i.e., be equal and opposite in sign, to first order. This variation in the firing rate of a neuron will reflect variations in the balance of the inputs.

3. We need a small fraction of active inputs, defined as $K$, where $1 << K << N$.

4. With a small number of inputs, the total variance, which is the sum of variances of the excitatory and inhibitory terms, can be high.

The input to the $i$th neuron is now the sum of outputs from excitatory cells, i.e., the $V^E_i(t)$, and inhibitory cells, i.e., the $V^I_i(t)$. Thus

$$\mu_i(t) = \mu^E_i(t) + \mu^I_i(t)$$

$$= \frac{1}{K} \sum_{j=1}^{K} W^E_{ij} V^E_j(t) + \frac{1}{K} \sum_{j=1}^{K} W^I_{ij} V^I_j$$

Let $W^E_{ij}$ be an excitatory input and $W^I_{ij}$ be an inhibitory input, simplified as above but now scaled to be large, where large is defines as order $\sqrt{K}$ rather than order 1. Thus

$$W^E_{ij} \rightarrow \sqrt{K} W^E_o$$

$$W^I_{ij} \rightarrow -\sqrt{K} W^I_o$$

where we implicitly fix the sign of the inhibition. The mean input under the assumed scaling is

$$\mu(t) = \sqrt{K} W^E_o \frac{1}{K} \sum_{j=1}^{K} V^E_j(t) - \sqrt{K} W^I_o \frac{1}{K} \sum_{j=1}^{K} V^I_j(t)$$

$$= \sqrt{K} \left( W^E m^E(t) - W^I m^I(t) \right)$$

where the order parameters are defined by

$$m^E(t) \equiv \frac{1}{K} \sum_{j=1}^{K} V^E_j(t) \quad \text{and} \quad m^I(t) \equiv \frac{1}{K} \sum_{j=1}^{K} V^I_j(t)$$
and we have assumed without loss of generality that the same number of excitatory and inhibitory inputs. The input is large if the excitatory and inhibitory terms do not cancel balance to within a factor of $\frac{1}{\sqrt{K}}$. The variance, following the derivation for the single input case, is

$$
\sigma^2 = \frac{1}{K} \sum_{i=1}^{K} \left( \left( \mu_i^E(t) - \langle \mu^E \rangle \right)^2 \right) + \frac{1}{K} \sum_{i=1}^{K} \left( \left( \mu_i^I(t) - \langle \mu^I \rangle \right)^2 \right) \quad (9.16)
$$

$$
= \frac{(\sqrt{K}W^E)^2}{K} m^E(1-m^E) + \frac{(\sqrt{K}W^I)^2}{K} m^I(1-m^I)
$$

$$
= (W^E)^2 m^E(1-m^E) + (W^I)^2 m^I(1-m^I).
$$

The important point is that there is no decrement as $K \to \infty$. Further, the variance remains nonzero for the special case of $W^Em^E = W^Im^I$, where the network is in "perfect" balance.

It is fair to ask if there is evidence to support this scaling, which would depend on a homeostatic mechanism. Barres and Reyes built networks in cell culture of different size and find scaling of the synaptic inputs scales as $K^{0.6}$, i.e., the synaptic potentials scale as $(1/\sqrt{K})^{1.2}$, close to the predicted value of $1/\sqrt{K}$ for strong inputs, as opposed to $1/K$ for weak input. Not bad!

### 9.1.3 Variance versus mean driven spiking

How do we interpret the mean and variance in terms of spike probability? We use the approximation of neuronal output as a Bernouli, i.e., $V = 1$ if the cell spikes and $V = 0$ if it does not. In the absence of noise the transition for 0 to 1 is sharp at $\mu = \theta$. How does the average probability of spiking smear when the variance is non-zero? The simplest possibility is to assume a Gaussian amplitude distribution so that

$$
m(t) = \frac{1}{\sqrt{2\pi\sigma}} \int_{\theta}^{\infty} dx \ e^{-(x-\mu)^2/2\sigma^2} \quad (9.17)
$$

$$
= \frac{1}{\sqrt{\pi}} \int_{-\infty}^{\mu-\theta/\sqrt{2\sigma}} dx \ e^{-x^2}
$$

$$
= 1 + \text{erf} \left[ \frac{\mu-\theta}{\sqrt{2}\sigma} \right] .
$$

When $\sigma$ is small compared to $\mu - \theta$, the transition from $m(t) = 0$ to $m(t) = 1$ is weakly smoothed, with

$$
m(t) \quad \sigma \ll \mu - \theta \quad 1 - \frac{\sigma}{\sqrt{2\pi} (\mu - \theta)} e^{-(\mu-\theta)^2/2\sigma^2} . \quad (9.18)
$$

When $\sigma$ is large compared to $\mu - \theta$, the transition from $m(t) = 0$ to $m(t) = 1$ is completely smoothed with

$$
m(t) \quad \sigma \gg \mu - \theta \quad \frac{1}{2} . \quad (9.19)
$$
An interesting issue is to have a fixed input and vary the noise. We see, numerically, that the spike rate increases monotonically with increasing values of $\sigma$ to a saturation value of $m = 0.5$ and that there is a roughly linear region of increase for mean rates between $m = 0.05$ and $m = 0.25$.

9.2 Circuit model

We now consider the consequences on the choice of connections in a network to maintain the balanced state. Consider a network of a population of interconnected excitatory (E) and inhibitory (I) cells. The full equations are

$$\tau_E \frac{dV^E_i(t)}{dt} + V^E_i(t) = \left[ \beta(\mu^E_i(t) - \theta^E_i) \right]_+$$
$$\tau_I \frac{dV^I_i(t)}{dt} + V^I_i(t) = \left[ \beta(\mu^I_i(t) - \theta^I_i) \right]_+$$

(9.20)

where $[\cdots]_+$ is the Heavyside function, $\tau_E$ and $\tau_I$ are the cellular time constant, $\beta$ is the conversion gain, and the $\theta^E_i$ and $\theta^I_i$ are thresholds. The inputs are

$$\mu^E_i(t) - \theta^E_i = \mu^E_{ext}(t) + \frac{1}{K} \sum_{j=1}^{K} W^{EE}_{ij} V^E_j(t) + \frac{1}{K} \sum_{j=1}^{K} W^{EI}_{ij} V^I_j(t)$$
$$\mu^I_i(t) - \theta^I_i = \mu^I_{ext}(t) + \frac{1}{K} \sum_{j=1}^{K} W^{II}_{ij} V^I_j(t) + \frac{1}{K} \sum_{j=1}^{K} W^{IE}_{ij} V^E_j(t).$$

(9.21)

As in the case of the model cell, we will scale the synaptic inputs by $\sqrt{K}$

$$W^{EE}_{ij} \rightarrow \sqrt{K} W^{EE}; \quad W^{II}_{ij} \rightarrow -\sqrt{K} W^{II}; \quad W^{EI}_{ij} \rightarrow -\sqrt{K} W^{EI}; \quad W^{IE}_{ij} \rightarrow \sqrt{K} W^{IE}$$

(9.22)

and, as will soon be clear, we need to similarly scale the external inputs by

$$\mu^E_{ext}(t) \rightarrow \sqrt{K} E m_{ext}(t) \quad \text{and} \quad \mu^I_{ext}(t) \rightarrow \sqrt{K} I m_{ext}(t)$$

(9.23)

where $E$ and $I$ are inputs of strength of $O(1)$. All together, we have

$$\mu^E_i(t) - \theta^E_i = \sqrt{K} E m_{ext}(t) + \frac{W^{EE}}{\sqrt{K}} \sum_{j=1}^{K} V^E_j(t) - W^{EI} \sum_{j=1}^{K} V^I_j(t)$$
$$\mu^I_i(t) - \theta^I_i = \sqrt{K} I m_{ext}(t) + \frac{W^{IE}}{\sqrt{K}} \sum_{j=1}^{K} V^E_j(t) - W^{II} \sum_{j=1}^{K} V^I_j(t).$$

(9.24)

In terms of the order parameters,

$$\mu^E(t) - \theta^E = \sqrt{K} E m_{ext}(t) + \frac{W^{EE}}{\sqrt{K}} \sum_{j=1}^{K} V^E_j(t) - W^{EI} \sum_{j=1}^{K} V^I_j(t)$$
$$= \sqrt{K} E m_{ext}(t) + \sqrt{K} W^{EE} m_E(t) - \sqrt{K} W^{EI} m_I(t)$$
$$= \sqrt{K} \left( E m_{ext}(t) + W^{EE} m_E(t) - W^{EI} m_I(t) \right)$$

(9.25)
and

\[ \mu_i(t) - \theta_i^i = \sqrt{K} I_m(t) + \frac{W_{EE}}{\sqrt{K}} \sum_{j=1}^{K} V_j^E(t) - \frac{W_{EI}}{\sqrt{K}} \sum_{j=1}^{K} V_j^I(t) \] (9.26)

\[ = \sqrt{K} \left( I_m(t) + W_{IE}^E m_E(t) - W_{II}^I m_I(t) \right) \]

As \( \sqrt{K} \to \infty \) the left hand side goes to zero and the equilibrium state will satisfy

\[ 0 \left( \frac{1}{\sqrt{K}} \right) = E m_{ext}(t) + W_{EE}^E m_E(t) - W_{EI}^I m_I(t) \] (9.27)

\[ 0 \left( \frac{1}{\sqrt{K}} \right) = I m_{ext}(t) + W_{IE}^E m_E(t) - W_{II}^I m_I(t). \]

The implication of this equilibrium condition is that the average input remains finite as the fluctuations remain large. This is the balanced state.

Solving the above gives relations for the equilibrium activity of the excitatory and inhibitory cells in terms of the external drive:

\[ m_0^E = \frac{W_{II}^E - W_{EI}^I}{W_{EE} W_{II} - W_{EI} W_{IE}} m_{ext}. \] (9.28)

and

\[ m_0^I = \frac{W_{IE}^E - W_{EE}^I}{W_{EE} W_{II} - W_{EI} W_{IE}} m_{ext}. \] (9.29)

We made many severe assumptions regarding this model, so these equations serve only to illustrate a few keys points.

1. The equilibrium values of activity \( m_0^E \) and \( m_0^I \) must be both positive and bounded by 1. This constrains the values of the synaptic weights.

2. Both the activity of the excitatory and the inhibitory populations are linearly proportional to the input, matching experimental observations of linear response with balanced networks.

3. A paradoxical effect is that increasing the external inhibitory input, i.e, \( I \), will increase both \( M_E \) and \( m_I \), can can in term increase \( \nu_I(t) \) and lead ti increased spiking of inhibitory cells. This is a feedback effect where reduced inhibitory input increase the activity of the excitatory cells that drive inhibition.

### 9.2.1 Stability

We return to the full network equations and look at the variation around the equilibrium value of \( m_E \) and \( m_I \). Taking the time constants, gains, and thresholds to be the same for the \( E \) and \( I \) populations and letting

\[ \delta m_E(t) = m_E(t) - m_0^E \] (9.30)

\[ \delta m_I(t) = m_I(t) - m_0^I \]
we have
\[
\frac{d}{dt} \delta m_E(t) + \delta m_E(t) = \left[ \beta \sqrt{K} \left( W_{EE} \delta m_E(t) - W_{EI} \delta m_I(t) \right) \right]_+ \quad (9.31)
\]
\[
\frac{d}{dt} \delta m_I(t) + \delta m_I(t) = \left[ \beta \sqrt{K} \left( W_{IE} \delta m_E(t) - W_{II} \delta m_I(t) \right) \right]_+.
\]

When the neurons are active, this reduces to the linear equations
\[
\frac{d}{dt} \delta m_E(t) + \delta m_E(t) = \beta \sqrt{K} \left( W_{EE} \delta m_E(t) - W_{EI} \delta m_I(t) \right) \quad (9.32)
\]
\[
\frac{d}{dt} \delta m_I(t) + \delta m_I(t) = \beta \sqrt{K} \left( W_{IE} \delta m_E(t) - W_{II} \delta m_I(t) \right).
\]

These linear equations are solved by taking \( \delta m_E(t) \propto e^{\lambda t} \), etc., so that
\[
(\lambda \tau + 1) \delta m_E(t) = \beta \sqrt{K} \left( W_{EE} \delta m_E(t) - W_{EI} \delta m_I(t) \right) \quad (9.33)
\]
\[
(\lambda \tau + 1) \delta m_I(t) = \beta \sqrt{K} \left( W_{IE} \delta m_E(t) - W_{II} \delta m_I(t) \right)
\]

which requires that
\[
\begin{vmatrix}
\beta \sqrt{K} W_{EE} - 1 - \lambda \tau & -\beta \sqrt{K} W_{EI} \\
\beta \sqrt{K} W_{IE} & -\beta \sqrt{K} W_{II} - 1 - \lambda \tau
\end{vmatrix} = 0 \quad (9.34)
\]

and leads to
\[
\lambda_{1,2} = \frac{1}{\tau} \left[ \frac{\beta \sqrt{K} (W_{EE} - W_{II})}{2} - 2 \pm \sqrt{\left( \frac{\beta \sqrt{K} (W_{EE} - W_{II})}{2} - 2 \right)^2 - \beta^2 K W_{IE} W_{EI}} \right]
\]
\[
K \to \infty \quad \frac{\beta \sqrt{K}}{\tau} \left[ \frac{W_{EE} - W_{II}}{2} \pm \sqrt{\left( \frac{W_{EE} - W_{II}}{2} \right)^2 - W_{IE} W_{EI}} \right]. \quad (9.35)
\]

The system is stable only if the real part of \( \lambda_{1,2} < 0 \). This implies
\[
W_{II} > W_{EE} \quad (9.36)
\]
along with \( W_{IE} W_{EI} > 0 \), which is always true. The response time of the system is shortened to \( \tau/(\beta \sqrt{K}) \).